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Research Article

Hitchhikers on dead shells: an unanticipated pathway of alien species invasion associated with discarded seafood remains at oyster tasting sites

Halyna Gabrielczak[1,2], Yuriy Kvach[1,3], Mikhail O. Son[1]

1 *Institute of Marine Biology, National Academy of Science of Ukraine, Italiyska St. 37, 65048, Odesa, Ukraine*
2 *Department of Ecology and Vertebrate Zoology, University of Lodz, Banacha 12/16, 90-237 Lodz, Poland*
3 *Institute of Vertebrate Biology of the Czech Academy of Sciences, Květná 170/8, 603 00, Brno, Czech Republic*
Corresponding author: Halyna Gabrielczak (halyna.morhun@biol.uni.lodz.pl)

Abstract

Shellfish mariculture, particularly of oysters, poses a significant risk for the introduction of non-native species into marine ecosystems. This study investigates the diversity of invertebrate species colonizing live and discarded oyster shells originating from a farm and oyster bar in the Tylihul Estuary, a region with active oyster farming. Advanced molecular techniques identified several invasive species associated with the discarded shells, including *Semibalanus balanoides*, *Austrominius modestus* and *Monocorophium insidiosum*. These taxa have not been previously documented in the region. Our findings indicate that macrofaunal composition differs between live and discarded oyster shells, and that the richness of invasive invertebrates associated with oyster shells is higher than expected. The discarded shells not only act as a substrate for colonization but also serve as potential vectors for biological invasions. We performed a Species-related Risk Assessment to identify the potential ecological impacts on local biodiversity and ecosystems of the invasive species associated with oysters. Our study proposes management strategies aimed at mitigating the risks associated with shells discarded by oyster bars. Our recommendations include informing recreational travellers and retailers about the implications of discarding shells into the water and advocating for the control of risks related to the use of shells as a construction material.

Key words: Biofouling, mariculture, marine ecosystems, oyster shells, risk assessment

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Introduction

Shellfish mariculture, i.e. the cultivation of marine organisms such as oysters, clams and mussels, has become a significant entry route of non-native species into marine ecosystems worldwide (Molnar et al. 2008; Cohen and Zabin 2009; Padilla et al. 2011; Carranza and Zu Ermgassen 2020; Avdelas et al. 2021; Tan et al. 2023). In Europe alone, more than 150 alien species have been linked to shellfish mariculture operations (Quayle 1964; Di Blasio et al. 2023).

One of the most commercially-important group of species in the fishery and aquaculture sectors is the oyster (FAO, http://www.fao.org). However,

the introduction of oysters, whether through mariculture or unintentionally through ballast water and self-settlement, has also facilitated the spread of their accompanying pathogens, parasites, and species inhabiting their shells (Quayle 1964; Verlaque et al. 2007; Tan et al. 2023). This complex interconnected web of potential invasions underscores the critical need for comprehensive risk assessment and management strategies (Chapman et al. 2003; Ruesink et al. 2005; Troost 2010). The Ukrainian region of the north-western Black Sea was long home to commercial oyster production based on the local European Flat Oyster (*Ostrea edulis* Linnaeus, 1758); however, the species was extirpated in the region in the 1970s (Zaitsev and Alexandrov 1998). Currently, oyster farming in Ukraine is based on the non-native Giant Asian Oyster *Magallana gigas* (Thunberg, 1793), which was first introduced to Crimea for maricultural purposes in 1980 (Zolotarev 1996). The species was also farmed in Romania, in the NW region of the Black Sea, in the period 2001–2003 (Zaharia and Crivăţ 2017). Since then, the popularity of Giant Asian Oyster farming has increased in Ukraine (Chetveryk and Kravchuk 2020).

To mitigate the risk of non-native species escaping into the environment, various approaches have been tried based on *inter alia* controlling ballast water, optimizing farm organization, and breeding sterile shellfish lines that cannot escape into the wild (Cohen and Zabin 2009). However, thorough ecological risk assessments are needed to ensure that any potential benefits obtained through future introductions outweigh the risks. While introducing non-native oysters can sometimes enhance ecological complexity (Green and Crowe 2014; Ahmed and Solomon 2016), the overall impact on the recipient ecosystem is often not well understood; in many cases, introduction can result in the displacement of native species and disruption of ecosystem functions (Ruesink et al. 2005).

The use of oysters as appetizers introduces another unexpected vector: discarded shells may carry live hitchhikers, i.e. organisms that attach to the shells and can survive their journey to new locations. This vector route is currently not considered in risk assessment or management approaches. Oyster farming has been implicated as a possible vector of introduction of the Korean Rockfish (*Sebastes schlegelii* Hilgendorf, 1880), a fish species from East Asia, into the Black Sea, including the north-western region (Mitov et al. 2020; Bilecenoğlu et al. 2023; Yağlıoglu et al. 2023; Kvach and Khutornoi 2025).

Oyster farming has recently emerged as a new industry in the northwest Black Sea region, significantly transforming its recreational and economic landscape. However, the outbreak of war led to the closure of beaches on the Black Sea, and the movement of tourists to oyster farms with bars located along the Tylihul Estuary. To meet the demand from tourists, the farms primarily raise single-line oysters, thus enhancing both growth efficiency and product quality; however, the farms typically buy oysters that have been grown elsewhere, and while the oyster industry has stimulated local tourism and economy, its ecological impacts remain largely underexplored.

Our present study investigates the influence of oyster farming on the local ecosystem, with a particular focus on the introduction and spread of invasive species resulting from the accumulation of discarded oyster shells from oyster bars in the Tylihul Estuary, a region with active oyster farming and seafood consumption. More specifically, we examine the diversity of invasive invertebrate species colonizing oyster shells in the estuary itself, and those sold in the oyster

bar. Our aim is to identify the vectors for invasion and determine biosecurity and environmental management strategies to counter them. Our study also reassesses the classification systems of these vectors, incorporating food tasting sites and their proximity to farms, in accordance with the Convention on Biological Diversity (CBD) (1995), a widely accepted framework for categorizing and managing biodiversity and its threats.

Materials and methods

Site

The Tylihul Estuary is the largest and deepest estuary in the northwestern Black Sea region, which separated from the sea by a sandbar in the 18th–19th centuries. The large catchment area (5,420 km^2), small width (up to 4.5 km) compared to its length (60 km), numerous long sandbars, and depth differences, ranging from 3–5 m in the northern part to 10–22 m in the southern part, complicate water exchange, and the degradation of river basins leads to a deficit in runoff. As a result, its hydrological regime is artificially regulated by a connecting channel, which has operational shortcomings that have repeatedly led to sharp changes in the salinity of the estuary (Tuchkovenko and Loboda 2014). Natural seasonal changes in salinity, which are mainly caused by river runoff, are limited, while sharp changes related to artificial hydrological conditions occur when, for example, access to seawater is closed or opened over a period of several years. During research conducted in the summer of 2023, the salinity of the estuary reached 29.7 PSU (practical salinity units).

The estuary is home to infrastructure related to an oyster farm as well as two small resort areas which attract tourists mainly with their oyster bars. One of these bars, located in the village of Kordon in the Odesa district (Fig. 1), have a wide tourist infrastructure with wooden boardwalks and piers extending into the water near the oyster bar. This allows visitors to eat oysters while standing on these structures and throw their shells directly into the estuary. As a result, a zone of discarded oyster shells with a radius of up to 5 m forms around the piers and wooden decks. This area is one of the research monitoring stations of the Institute of Marine Biology MAS of Ukraine (IMB), with observations taking place each season to ensure continuous monitoring of ecosystem changes, but it covers sublittoral mixed sediments and macrophytes, not the littoral zone directly adjacent to the resort infrastructure. The second resort area is in the village of Ukrainka in the Mykolaiv region. It has a different internal layout and the beach area preferred by tourists is more separated from the oyster bar.

Field studies

The analysis included three sources of primary material, shown in Table 1 and in the text. All material was collected during the expedition on June 16, 17, 2023 in the village of Kordon in the Odessa region (46.8343°N, 31.1038°E).

The first included living epibionts on dead oyster shells collected in the littoral zone of the Tylihul Estuary near the oyster bar. Such epibionts also included both macroinvertebrates and spawning fish found inside the shells deposited at the bottom of the estuary. These specimens were extracted from the oysters and

Figure 1. Photos of site: Tylihul Estuary oyster bar near an oyster farm in Kordon village.

Table 1. Macrofauna composition on oysters from bottom of Tylihul estuary near the oyster bar and nearby solid substrates. The varying levels of abundance across species are represented by: + = single individual, ++ = 2–10 individuals, +++ = more than 10 individuals.

Species	Status	Oyster shells discarded at the bottom of the estuary	Epibionts, which attached to live oysters from the oyster bar kitchen.	Other hard substrates (piers, moorings)
Austrominius modestus (Darwin, 1854)	alien	++	++	
Balanus trigonus Darwin, 1854	alien	+		
Semibalanus balanoides (Linnaeus, 1767)	alien	++	++	
Gammarus aequicauda (Martynov, 1931)	native	++		+++
Idotea balthica (Pallas, 1772)	native	++		+++
Lekanesphaera monodi (Arcangeli, 1934)	native	++		+++
Monocorophium insidiosum (Crawford, 1937)	alien	+++		
Mytilaster lineatus (Gmelin, 1791)	native	+++		+++
Gobius niger Linnaeus, 1758	native	+		
Parablennius tentacularis (Brünnich, 1768)	native	+		
Spirorbidae	alien	*	+	

* A few calcareous polychaete tubes were found on the valves, but in the part of them that was opened in the laboratory, no living polychaetes were found.

subjected to a thorough examination. The second source included live oysters from the oyster bar kitchen and epibionts (attached macroinvertebrates) found on their shells. The third source included macroinvertebrates found on hard substrates of wooden boardwalks and piers extending into the water near the oyster bar. The analysis also included the macrofauna present on live oysters sold on the beach.

The second resort area, in the village of Ukrainka in the Mykolaiv region (46.7474°N, 31.1680 °E) was studied during the expedition on August 16, 2023. In this area, we did not find any accumulations of discarded oyster shells or new alien species, and this area will not be discussed further in our paper.

Sampling underwater was conducted by snorkelling, allowing for direct access to the underwater environment. The identity of any invasive invertebrate species colonizing the oyster shells, and of the living oysters sold in the oyster bar were confirmed using molecular techniques.

Molecular studies

All animals found on the shells, together with a small part of the oyster muscle tissue, were dissected and preserved in 96% ethanol for molecular study. The specimens were deposited in the collection of the IMB.

Genomic DNA was isolated at the Department of Ecology and Vertebrate Zoology at the University of Lodz (Poland) using the Chelex buffer method (details in Casquet et al. 2012). DNA barcoding was performed based on the mitochondrial *cox1* gene (Hebert et al. 2004). The DNA was amplified using HCO2198 and LCO1490 primers (Folmer et al. 1994) under the following PCR protocol: 3 min – 94 °C; (30 s – 94 °C, 1:30 min – 45 °C and 1 min – 72 °C) × 5; (30 s – 94 °C, 1:30 min – 51 °C and 1 min – 72 °C) × 35; 5 min – 72 °C (Hou et al. 2007). The amplicons were purified with exonuclease I (20 U/µl; EURx) and Fast Polar-BAP alkaline phosphatase (1 U/µl, EURx).

The material was subjected to Sanger sequencing (Macrogen Inc); the results were analysed in online GenBank repositories using BLAST (https://www.blast.ncbi.nlm.nih.gov) and BOLD identification to find similarities. The data were registered in BOLD under dataset DS-OYSTER. The sequences were assigned BINs (Barcode Index Numbers) based on the genetic distance to other similar sequences in the database (Ratnasingham and Hebert 2013). The algorithms used to assign BINs are described in Ratnasingham and Hebert (2013); for invertebrates, a genetic distance greater than 2% is assumed to indicate a different Barcode Index Number. A map of the geographic distribution data of the identified *M. gigas* and *Monocorophium insidiosum* (Crawford, 1937) sequences and those available in the BOLD System (www.barcodinglife.org, Suppl. material 1) was performed in QGIS v.3.0.8.

Species-related risk assessment

The risks associated with invasion by newly-discovered alien species were determined by three approaches: identification of invasion pathways, assessment of potential species-related risks (invasiveness) and the observed level of biological pollution.

Any pathways used for invasion were identified using the CBD Pathway Classification framework (Harrower et al. 2017; Tsiamis et al. 2017).

Invasiveness was assessed using the Species-specific Biopollution Risk (SBPR) index (Panov et al. 2009). This index is based on a general assessment of the degree of invasiveness of a specific alien species according to its potential for high risk for dispersal (HRD), high risk for establishment in a new environment (HRE), and high risk of causing ecological and negative socio-economic impacts (HRI). The HRD, HRE and HRI information of a particular alien species is widely available in any publications associated with its introduction; how to use these data to inform the SBPR index are provided within the original methodology.

Based on these three risk aspects, a species can be classified according to a five-point risk assessment scale in line with the Water Framework Directive (Directive 2000). This risk-based approach is used when formally including an alien species in the Grey, White, and Black Lists: the Grey List indicates that a species is a priority for research and status clarification, and the Black List for environmental management. The White List includes species that are not a priority for management.

The level of biological pollution of the Tylihul Estuary caused by each exotic species detected was assessed using the BioPollution Level (BPL) index; this estimates

the biological pollution of a particular water body based on four expert judgements: abundance/distribution class, impact on native species and communities, impact on habitats, and impact on ecosystem functioning (Olenin et al. 2007).

For both SBPR and BPL indices, the term 'experts' hereinafter refers to the authors of the article who conducted the assessment procedures.

Results

The live oysters from the Tylihul Estuary oyster bar were found to be *M. gigas* (this lineage is partially assigned as *Crassostrea corteziensis* (Hertlein, 1951), when registering primary data in the Genbank system – https://www.ncbi.nlm.nih.gov/Genbank), a species recognized for its commercial value in the region. A comparison with the sequences available in the public database (Suppl. material 1) indicated 236 sequences, which collapsed to 73 haplotypes. Of these, one haplotype was found to be particularly widely distributed; this includes our oyster sequence and 122 others (Fig. 2).

In addition to the oysters, our molecular analyses identified three invasive invertebrate species inhabiting the surface of the live oysters from the bar kitchen:

1. *Semibalanus balanoides* (Linnaeus, 1767) (Balanomorpha, Balanidae): The sequence of our species was found to belong to the Barcode Index Number (BIN): BOLD:AAA3935. Comparative haplotype assessment indicated a strong genetic similarity with specimens collected from Dal'nie Zelentsy in the Murmansk region of Russia and with others from the North Sea, suggesting a widespread distribution across diverse marine environments.
2. *Austrominius modestus* (Darwin, 1854) (Balanomorpha, Elminiidae): This species was identified under BIN: BOLD:ABX4245.
3. *Monocorophium insidiosum* (Amphipoda, Corophiidae): Two distinct genetic lineages of this species were detected, corresponding to BINs BOLD:AAE1628 and BOLD:AAE9749. Remarkably, these lineages co-occurred in numerous locations, including both in their native habitats in the North Atlantic Ocean and invasive populations established in the Pacific Ocean and Black Sea (Fig. 2).

The species composition and prevalence of all sources of oyster are summarized in Table 1 and Figs 3, 4.

The shells in the estuary were found to be home to fewer exotic species; however, the analyses revealed native species of molluscs and crustaceans occupying the surfaces, with gobies and dogfish settling and spawning in the oyster shells (Fig. 5). The hard substrates presented slightly higher numbers of native species, and no invasive species were detected.

While our study focused solely on macroinvertebrates and fish, it is important to note that the oysters also host a variety of meiobenthos (mites, copepods), microalgae, and macrophytes.

Species-related risk assessment

Identification of the invasion pathway

According to the CBD classification (Harrower et al. 2017), this case can be identified as pathway "3.3 Food contaminant (including live food)" of the

Figure 2. Spreading of the haplotype of *Magallana gigas* found in Tylihul Estuary (upper map) and spreading of two distinct genetic lineages (green – BOLD:AAE1628, red – BOLD:AAE9749) of *Monocorophium insidiosum* (lower map). Our material is marked with a star. Dots inside the continent in Canada and South Africa (upper map) are from sequences of animals sold in markets.

"Transport – Contaminant" category (species introduced unintentionally or accidentally through the movement of other organisms or organic materials and products). It cannot be defined as "Release in Nature" (pathway "1.3 Fishery in the wild"), "Escape from confinement" (pathways "2.2 Aquaculture / mariculture" and "2.11 Live food and live bait"), or "Transport – Contaminant" (pathway "3.4 Contaminant on animals, excluding parasites and species transported by host and vector") because the identified invertebrates were not the target species used by humans, like the oysters themselves, but only hitchhikers carried along with the target species.

In addition, 3.4 Contaminants on animals (excluding parasites and species transported by host and vector), refers to situations where a species is transported to a location where it was farmed or raised with associated infrastructure and

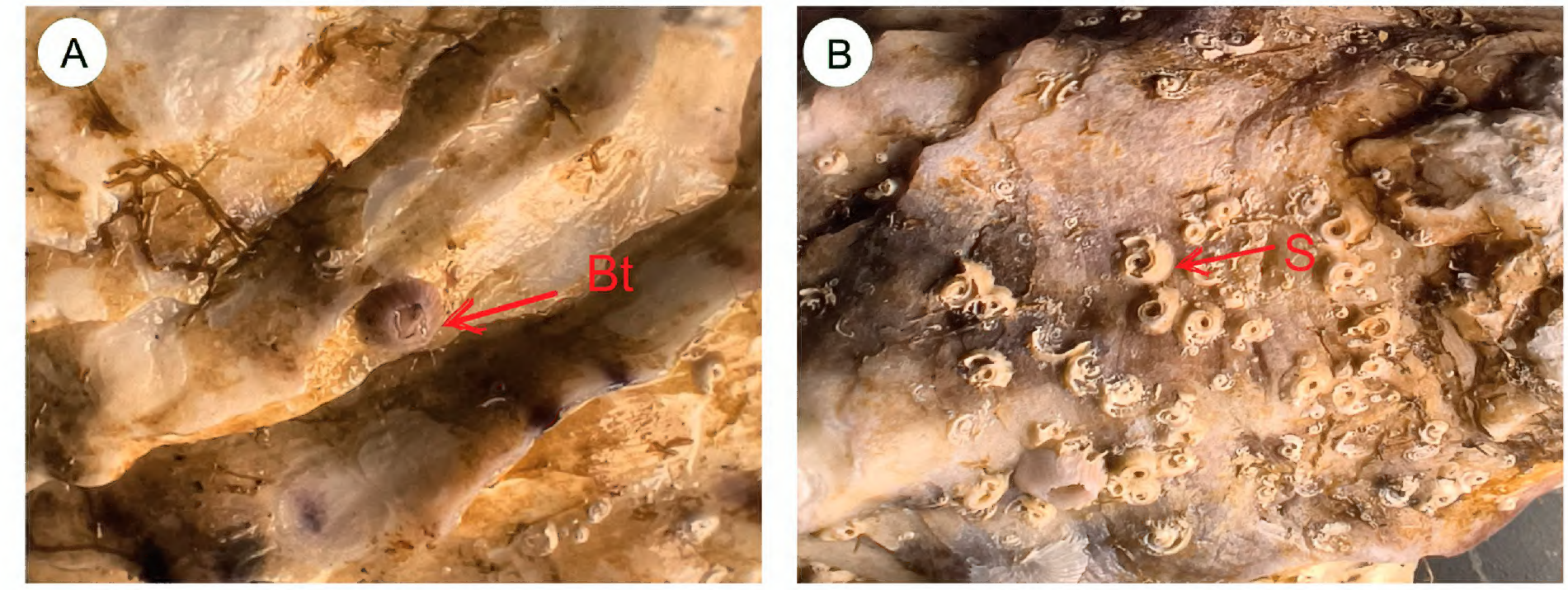

Figure 3. Biofouling fauna on sold oysters (**A, B**) and on living oysters on natural substracts in the Tylihul Estuary (**C, D**). Abbreviations: Bt = *Balanus trigonus*, S = Serpulidae, Sb = *Semibalanus balanoides*, Am = *Austrominius modestus*, Ml = *Mytilaster lineatus*.

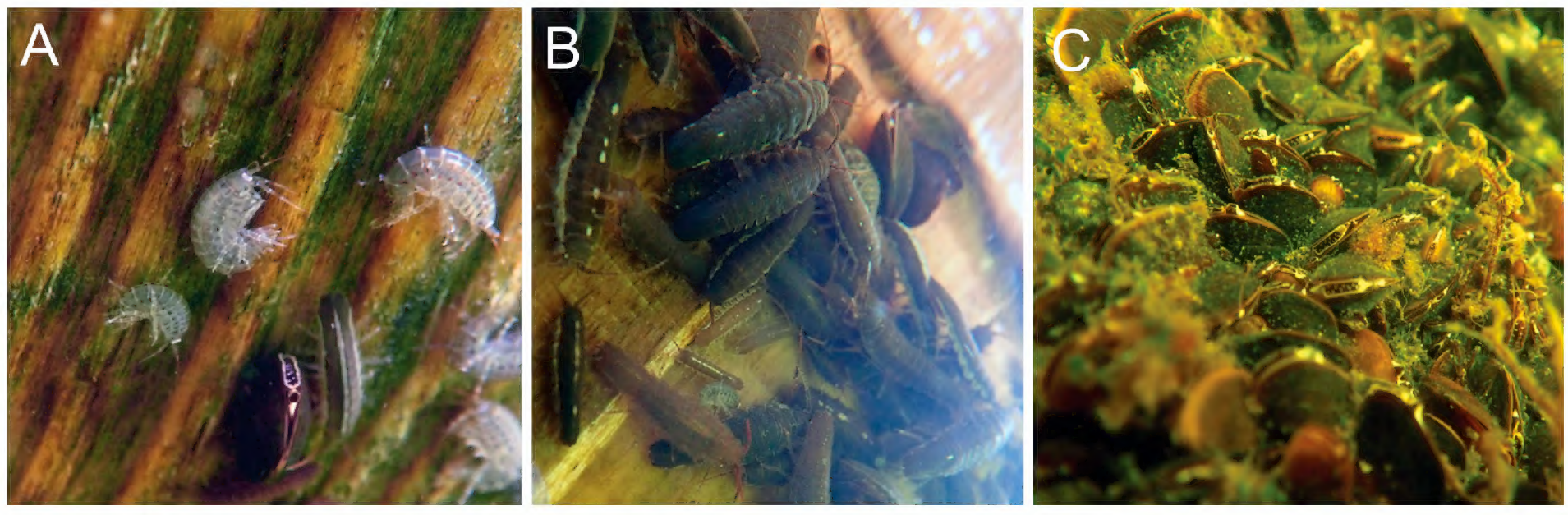

Figure 4. Native species of mollusks and crustaceans which occupy hard substrates (piers, moorings, etc.) in the Tylihul Estuary and could be impacted by invasive species. **A.** *Gammarus* spp.; **B.** *Idotea balthica*; **C.** *Mytilaster lineatus*.

control methods; in this case, the oysters were transported to where they were directly sold and consumed.

These pathways form part of the expert opinion for the SBPR index assessment of the species identified in the Tylihul Estuary. In addition to the pathway identified herein, these species have also been found to use the following invasion routes:

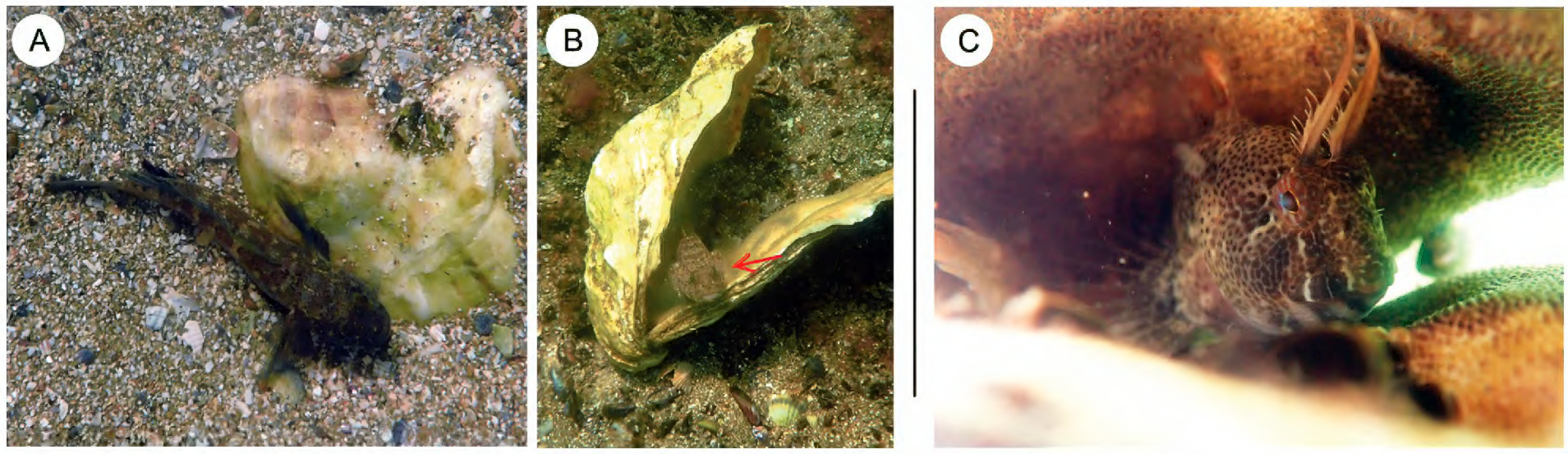

Figure 5. Native gobies and dogfish settling and spawning in the oyster shells in the Tylihul Estuary. **A, B.** *Gobius niger*; **C.** *Parablennius tentacularis*.

Austrominius modestus: "4.4 Hitchhikers on ship/boat (excluding ballast water and hull fouling)", "4.8 Ship/boat ballast water", "4.9 Ship/boat hull fouling", "6.1 Natural dispersal across borders of invasive alien species that have been introduced through pathways 1 to 5" (Carlton et al. 2011; Glenner et al. 2021).

Semibalanus balanoides: "4.8 Ship/boat ballast water", "4.9 Ship/boat hull fouling", "6.1 Natural dispersal across borders of invasive alien species that have been introduced through pathways 1 to 5" (Carlton et al. 2011; Glenner et al. 2021).

Monocorophium insidiosum: "4.9 Ship/boat hull fouling", "3.4 Contaminant on animals (excluding parasites and species transported by host and vector)" (Wasson et al. 2001; Oliver et al. 2007).

Invasiveness

The assessed species differ in the level of risk according to the Species-specific Biopollution Risk (SBPR) index (Panov et al. 2009) (Table 2). Only one species, *A. modestus*, has demonstrated risk for all three criteria used in the index (SBPR level = 4), indicating that it can be blacklisted as an invasive species of high priority for management.

Biological pollution

The analysed species currently demonstrate low biological pollution according to the BioPollution Level (BPL) index. This is to be expected given their highly-localized distribution and small numbers (Abundance/Distribution Class "B" – species occurs in moderate numbers in one locality) (Table 3).

According to the methodology (Olenin et al. 2007), classes C0, E0, and H0 indicate no observable effect based on the relevant indicators. Classes H1 and E1 show a weak impact based on the relevant indicators (alteration without reduction of spatial extent of a habitats and weak changes with no loss or addition of new ecosystem functions). The differences in "Impact on habitats" and "Impact on ecosystem functioning" noted between species can be attributed to the fact that barnacles are fouling filter feeders; these act as ecosystem engineers and represent a deficient functional group of organisms in the studied water body.

Table 2. Evaluation of criteria used to determine the Species-specific Biopollution Risk index according to Panov et al. (2009).

Species	High risk for dispersal	High risk for establishment in a new environment	High risk to cause ecological and negative socio-economic impacts	Species-specific Biopollution Risk index
Austrominius modestus	Pathway diversity, different regions of invasions (Glenner et al. 2021; Carlton et al. 2011; this study)	Wide euryhaline and eurythermal; wide range of invaded habitats (Glenner et al. 2021)	Competition with other barnacle species, transformation of ecosystem (O'Riordan et al. 2020)	4 points, high level of invasiveness
Semibalanus balanoides	Pathway diversity, different regions of invasions (Glenner et al. 2021; Carlton et al. 2011; this study)	No	No	1 point, low level of invasiveness
Monocorophium insidiosum	Pathway diversity, different regions of invasions (Wasson et al. 2001; Oliver et al. 2007; this study)	Established invader in different regions and habitats (Wasson et al. 2001; Oliver et al. 2007; Grintsov 2018; this study).	No	2 points, moderate level of invasiveness

Table 3. Evaluation of the criteria used to determine the BioPollution Level according to Olenin et al. (2007). See text for the meaning of letters and number used in the classification.

Species	Abundance/ Distribution Class	Impact on native species and communities	Impact on habitats	Impact on ecosystem functioning	BioPollution Level
Austrominius modestus	B	C0	H1	E1	1 point, weak
Semibalanus balanoides	B	C0	H1	E1	1 point, weak
Monocorophium insidiosum	B	C0	H0	E0	1 point, weak

Discussion

Oysters in the Black Sea

The Black Sea is home to considerable numbers of cultivated *M. gigas* and *Crassostrea virginica* (Gmelin, 1791), both of which have ranges expanding into natural habitats. Although the *M. gigas* found in the studied Tylihul oyster bar have commercial value, it is important to recognize that it also has invasive potential and can act as a vector for the spread of other species; as such, it could pose a significant threat to the local ecosystem, and measures should be taken to prevent its escape into the wild. The penetration of *M. gigas* into other parts of the Black Sea with the emergence of breeding or potentially breeding wild populations has already been recorded in several regions of the Black Sea outside the study area (Aydin and Gül 2021). Indeed, this commercial oyster species (Kim et al. 2015) has been repeatedly identified as an invasive species in natural environments in other parts of the world (Liu et al. 2011; Pejovic et al. 2016; Ren et al. 2016).

Newly-introduced species and the biofouling community on dead oyster shells

The communities present on the dead oyster shells were found to comprise alien species, probably introduced with the oysters as accidental hitchhikers. These were accompanied by large numbers of native invertebrate species, which are typical

inhabitants of the Tylihul Estuary (Varigin 2023) and were also found on other hard substrates in the vicinity.

Two new alien species were identified on the discarded shells, *S. balanoides* and *A. modestus*, indicating that the shells represent a new introduction vector for the Black Sea. While these species have been reported elsewhere (Carlton et al. 2011), their association with oyster shells and subsequent introduction through discarded remains is a novel finding. The amphipod *M. insidiosum* has multiple introductions into the Black Sea: it was previously listed from Crimea (Shadrin and Anufriieva 2013; Grintsov 2018) and from the eastern Turkish coast (both genetic BINs: BOLD:AAE1628, BOLD:AAE9749) but without discussion of the vectors of introductions.

The detected species in Tylihul Estuary exhibit considerable divergence with regard to their origin, for example, the Australasian *A. modestus* compared to the boreal circumpolar *S. balanoides* and *M. insidiosum*. This diversity has various implications for their distribution dynamics and prognoses in the context of climate change (Jones et al. 2012; Crickenberger and Wethey 2018; Herrera et al. 2019; Glenner et al. 2021). The cold-water habitat of the Black Sea, which in its most desalinated northwestern part was traditionally accompanied by periodic icing, historically prevented invasions by warm-water tropical and subtropical alien species such as *A. modestus*. On the contrary, arctic-boreal species, which often do not survive in the Mediterranean Sea, have historically been present in the Black Sea fauna as a permanent element (Zaitsev and Mamaev 1997). However, climate change over the last two decades has dramatically altered the situation, and warm-water alien species, previously found only sporadically in the Black Sea, are beginning to form stable populations, as shown, for example, for the Blue Crab *Callinectes sapidus* Rathbun, 1896 (Kvach et al. 2025a). Interestingly, among the other alien species previously recorded in the Tylihul Estuary, those which are characteristic of hard substrate communities were absent on the oysters. In particular, *Arcuatula senhousia* (Benson, 1842), a recent invader actively colonizing the region (Zhulidov et al. 2021; Son et al. 2023; Varigin 2023), was only identified in clusters of filamentous algae and was present at a greater depth than oyster shell clusters. In addition, the crab *Rhithropanopeus harrisii* (Gould, 1841), characteristic of estuaries of the region (Makarov 2004; Son et al. 2013), was not observed; the species may have disappeared from the Tylihul Estuary, or become extremely rare, following a sharp increase in salinity.

An interesting feature is that oyster valves were actively exploited as refuges by native fish species. Bivalve shellfish aquaculture is a ready source of shells as settlement substrate, which has a significant impact on the value of habitats for fish and mobile invertebrates (Theuerkauf et al. 2022). It is a typical spawning substrate used by demersal fish such as gobiids and blenniids (Inui et al. 2010; Tiralongo et al. 2016; Prakash and Kumar 2025). Gobiids are one of the most numerous fish components in the Tylihul Estuary (Kvach 2004; Snigirov et al. 2017). Both fishes that occurred in the locality (*Gobius niger*, *Parablennius tentacularis*) are native for the Black Sea (see Movchan 2011; Snigirov et al. 2020). The Black Goby was registered in the estuary in the last decade as a common species (Snigirov et al. 2017), while the Tentacled Blenny is common in adjacent sites of the Black Sea (Khutornoy and Kvach 2019; Snigirov et al. 2020) but registered in the Tylihul Estuary for the first time. Overall, the observed pattern is consistent with similar scenarios noted in various

other regions: the large, textured shells provide hard substrate and refuges for a variety of benthic species, both attached fouling and mobile fish and crustaceans, which can support a diverse biological community (Kingsley-Smith et al. 2012; Walles et al. 2015; Png-Gonzalez et al. 2021). In the Tylihul Estuary, where natural hard substrates are scarce and no shipping ports or other large-scale hydraulic structures are present, even small amounts of such hard substrates attract invasive species and affect biodiversity. However, at their current level of distribution, new species only present weak and localized levels of biological pollution.

Marine food residues as a pathway

Current aquaculture risk assessments often overlook marine food residues as a potential vector. However, oyster bars merit particular consideration, whether they are separated from farming locations or not. If they are present in areas near farms, the accumulation of discarded shells can drive the spread of invasive species, while if they are located away from the farms, discharges can create distinct target biotopes for invasive species. A similar risk may come from consuming oysters at beach parties or cocktail bars that do not specialize in seafood but just sell it.

There is hence a need to reassess the current system of pathway classification by incorporating food tasting sites (bars) and their proximity to farms. Until now, the "3.3 Food contaminant (including of live food)" pathway has been a well-known route for terrestrial organisms (Montagnani et al. 2022) but was not considered relevant for aquatic invertebrates: in over 200 cases of invasion by target species or associated companion species following escape from aquaculture/mariculture, or by transport to breeding and rearing sites, not a single case in Europe has been identified based on the CBD Pathway Classification (Pergl et al. 2020).

In an inventory of biological invasions taking place in the seas of Europe, more than 150 identified taxa (genera or species) of animals, plants and microorganisms were associated with edible farmed molluscs, mainly oysters (Di Blasio et al. 2023).

In the Tylihul estuary, several exotic barnacles were observed, but these were not associated with oyster cultivation (Di Blasio et al. 2023). Such species are often actively dispersed by shipping. Other pathways for invasion are possible, but these are usually only discussed when shipping is unlikely or when direct evidence of another route is available. This bias in assessing pathways of introduction is a recognised source of difficulty in invasion science (Katsanevakis et al. 2013; Katsanevakis and Moustakas 2018).

In contrast, *M. insidiosum* invasions appear to be potentially associated with cultivated molluscs. Such invasions have been associated with oyster mariculture in various regions including Irish lagoons and along the Pacific coast of North America (Wasson et al. 2001; Oliver et al. 2007). Its precise invasion history in the Black Sea remains unclear, but for the first few years after its discovery (1999-2001), it was only observed on mussel collectors (Grintsov 2018).

Shell recycling as a dependent pathway

Oyster shell recycling, i.e. the use of empty shells collected by restaurants or consumers to replenish substrate in the sea, is a widespread practice in North America, where there are many such environmental programs ranging from localized small-scale returns of shells to the sea to the construction of huge oyster reefs from

empty shells acting as breakwaters (Chowdhury et al. 2019; Kimbro et al. 2020; Birney et al. 2021; Petrolia and Mohrman 2024). However, it is important to note that attempts to imitate the oyster reefs natural to the region, i.e. those formed by *Crassostrea sensu lato*, may use many shells from other cultivated species.

Generally, shell recycling is not a common practice in Europe; however, as part of initiatives by local activists and NGOs, oyster shells from oyster bars on the Tylihul Estuary were used to create experimental artificial reefs, which in 2020 were installed in the Black Sea near the Kinburn Spit (TSN 2020).

In situ evidence of species transfers taking place in this way, and the associated recommendations for quarantine of empty shells, concern mainly pathogens harmful to live oysters (Bushek et al. 2004; Brumbaugh and Coen 2009). However, studies also highlight the possibility of the transfer of toxic unicellular algae present on the shells (Brumbaugh and Coen 2009), which has been confirmed experimentally by Hégaret et al. (2008).

Such transfers can be classified as pathway "3.10 Transportation of habitat material (soil, vegetation, wood…)" (Harrower et al. 2017), although the shells were probably not previously used as an underwater building material. This differs from the pathway described before (i.e. 3.3 Food contaminant, incl. live food) in that the shells are transported as building material, during which they are subjected to temporary drying that kills most aquatic invertebrates present. Nevertheless, it seems that this pathway takes place in the studied region and may become an additional route in the Black Sea basin, which is dependent on the transportation of oysters as live food. Potentially, if found, harmful algae and bacteria that are introduced can also be classified under other categories, such as 'Transport – Contaminant'. Harmful algal outbreaks can directly impact health and profitability by poisoning.

The potential use of discarded clamshells in building projects like artificial reefs may hence pose a risk of species invasion. Although the used shells were left for a long time at high temperatures, killing any macrozoobenthos, it is possible that any microalgae present may well survive. Additionally, clamshells can serve as stepping stones for the secondary spread of invasive species, even though they start completely clean.

Peculiarities of the Black Sea – methods of management at the institutional level

The lower salinity of the Black Sea typically acts as a barrier against certain oceanic species (Gomoiu et al. 2002). However, the Tylihul Estuary has undergone repeated changes in salinity which have destroyed the original communities (Gogaladze et al. 2021) and may have created a unique opportunity for new species to thrive.

This issue has been exacerbated by the closure of the Black Sea for recreation purposes due to the Russian-Ukrainian war (Kvach et al. 2025b). As a result, estuary-based activities have experienced increased demand and higher numbers of recreational visitors and tasting sites have purchased additional oysters from diverse import sources to meet the demand.

Hence, an effective management strategy is required. Experiments increasingly show that localised strategies for countering biological invasions are failing and efforts need to be redirected towards large-scale preventive approaches, in particular, the formation of a common European management area (Kurtul and Haubrock 2024). Analyses of

invasion pathways in European marine ecosystems have found aquaculture-related invasions to be managed most effectively via strict national regulations (Katsanevakis et al. 2013). It is important to note that the live food-related pathway of invasion is not driven by production, a part of national economic activity, but by international and domestic trade, separate spheres of control and management (Hulme 2021).

Until recently, Ukrainian legislation included very few direct regulations for the management of invasive species, with the exception of the phytosanitary control system. Some commitments that relate to monitoring, research, or general management strategies are included in various signed international agreements. Among these, the following agreements may affect marine and estuarine species associated with mariculture: the Convention on Biological Diversity (1995), ratified in 1995, the Convention on the Conservation of European Wildlife and Natural Habitats or the Bern Convention (Council of Europe 1996), ratified in 1996, and the Convention on the Protection of the Black Sea against Pollution (United Nations Environment Programme 1994), ratified in 1994.

In addition, explicit standards for preventing biological invasions by controlling relevant pathways are given in 2004 in the International Convention for the Control and Management of Ship Ballast Water and Sediments (International Marine Organization 2004) and the Convention on International Trade in Endangered Species of Wild Fauna and Flora (ratified in 1999).

In the last few years, Ukraine has undergone a large-scale modernization of legislation related to alien species as part of the integration of the legislative norms and principles of the European Union. A number of changes have already been implemented, including mandatory monitoring of invasive species in inland, transitional, coastal, and marine waters, the integration of regulations and lists of dangerous alien species adopted into legislation by the European Commission (Katsanevakis et al. 2023), and the adoption of several national conservation strategies.

This has been accompanied by the comprehensive integration of European regulations regarding the management of invasive species directly into Ukrainian legislation concerning aquaculture, fishery, Industrial Fishing and Water Conservation, protection of flora and fauna, and the management of protected areas. The Institute of Marine Biology (NAS) is an expert organization coordinating bills and official documents in these areas.

The planned legislation fundamentally tightens border control over the movement of invasive species and the possibility of their use in aquaculture. It also establishes obligations for fishery reclamation, which includes the removal or destruction of invasive species that threaten aquaculture. Bulgaria and Romania have already performed similar procedures as part of the EU entry procedures (Băncilă et al. 2022), as are many other countries in the Black Sea region.

The new Ukrainian legislation will not be retroactive, and a complete ban on the use of invasive species in aquaculture will not apply to previously-introduced species. As such, *M. gigas*, which has traditionally been used in local mariculture (Massa et al. 2021), will not be completely banned, despite the fact that in the last decade, it has clearly exhibited the characteristics of an invasive species in the Black Sea, as well as in Europe as a whole (Anglès d'Auriac et al. 2017; Krapal et al. 2019; Aydin et al. 2021; Băncilă et al. 2022).

However, other Crassostreinae may be prohibited for import into Ukraine if they are included in the lists of controlled species. It should be kept in mind, however, that alien species that are valuable bioresources, especially in the con-

text of food security, can be subject to inclusive management approaches in the form of various relaxations in control and eradication (Kourantidou et al. 2022; Gozlan et al. 2024).

Invasion could also be prevented by including potential hitchhikers in the lists of controlled invasive species. This is a feasible approach that requires research on oysters from various commercial lots present on the local market, although a pan-European project covering both importing and exporting countries would be desirable. Preliminary visual inspections indicate that different commercial brands of Pacific Oysters originating from various growing regions exhibit significant variation in their fouling organisms (Fig. 6). These fouling organisms primarily include barnacles, bryozoans, polychaetes, sponges, ascidians, and hydrozoans.

Recent studies of the Pacific Oyster industry have primarily focused on growth (Alunno-Bruscia et al. 2011; Devos et al. 2015), mortality (Kochmann and Crowe 2014; Schmitt et al. 2013), and viral infections (Dundon et al. 2011; Roque et al. 2012; Degremont et al. 2013; Mortensen et al. 2016); however, few genetic metabarcoding studies have examined biofouling in oyster farms. Studies based on eDNA may be useful for marine fishery management and ecosystem monitoring (Gilbey et al. 2021). Indeed, eDNA tools have been developed to detect the most harmful invasive non-native marine species for *Ostrea edulis* Linnaeus, 1758, and support its population restoration (Markus et al. 2021), or to detect wild oysters themselves (e.g. Coutts et al. 2022; Dugal et al. 2024;). Yet, there is lack of data on covering biofouling species on cultivated populations.

After inventory, any identified hitchhikers must undergo a Species-related Risk Assessment. In Ukraine, it is recommended that such aquatic invasive species should be subjected to the Institute of Marine Biology (NAS) risk assessment scheme, which is based on a Species-specific Biopollution Risk index. The inclusion of such species in pan-European or national lists of controlled species will provide legislative obligations for local administrations, business owners or other natural resource users to prevent invasions, remove or destroy introduced organisms, or develop management programs (Katsanevakis et al. 2023).

Possible approaches for the control of oyster epibionts at the local level

It should be noted that controlling oyster epibionts is unlike managing non-native species. The presence of epibionts influences both the marketability of the oyster at the time of sale (Mizuta and Wikfors 2019) and can cause problems with aquaculture, such as affecting population size, health and productivity, impacting economic costs, and causing general technical difficulties (Adams et al. 2011).

Control methods can also be divided into two groups. The first, biofouling removal or *punishment*, involves directly cleaning the oysters by various methods, such as mechanical scraping, scrubbing, brushing, pressure washing, drying and ultraviolet irradiation, dipping into fresh, high-salt or chlorinated water, and manual removal of the most unattractive specimens (Adams et al. 2011; Mizuta and Wikfors 2019). In addition, the cultivation process can be controlled by decisions regarding engineering, equipment and procedures, cleaning and waste behaviour, and a choice of cultivation regime (Adams et al. 2011).

Punishment by mechanical scraping and pressure washing should ensure that 'elite' specimens sold in restaurants or shops meet local shape and size standards and are free of sediments and fouling such as barnacles, hydroids, other bivalve

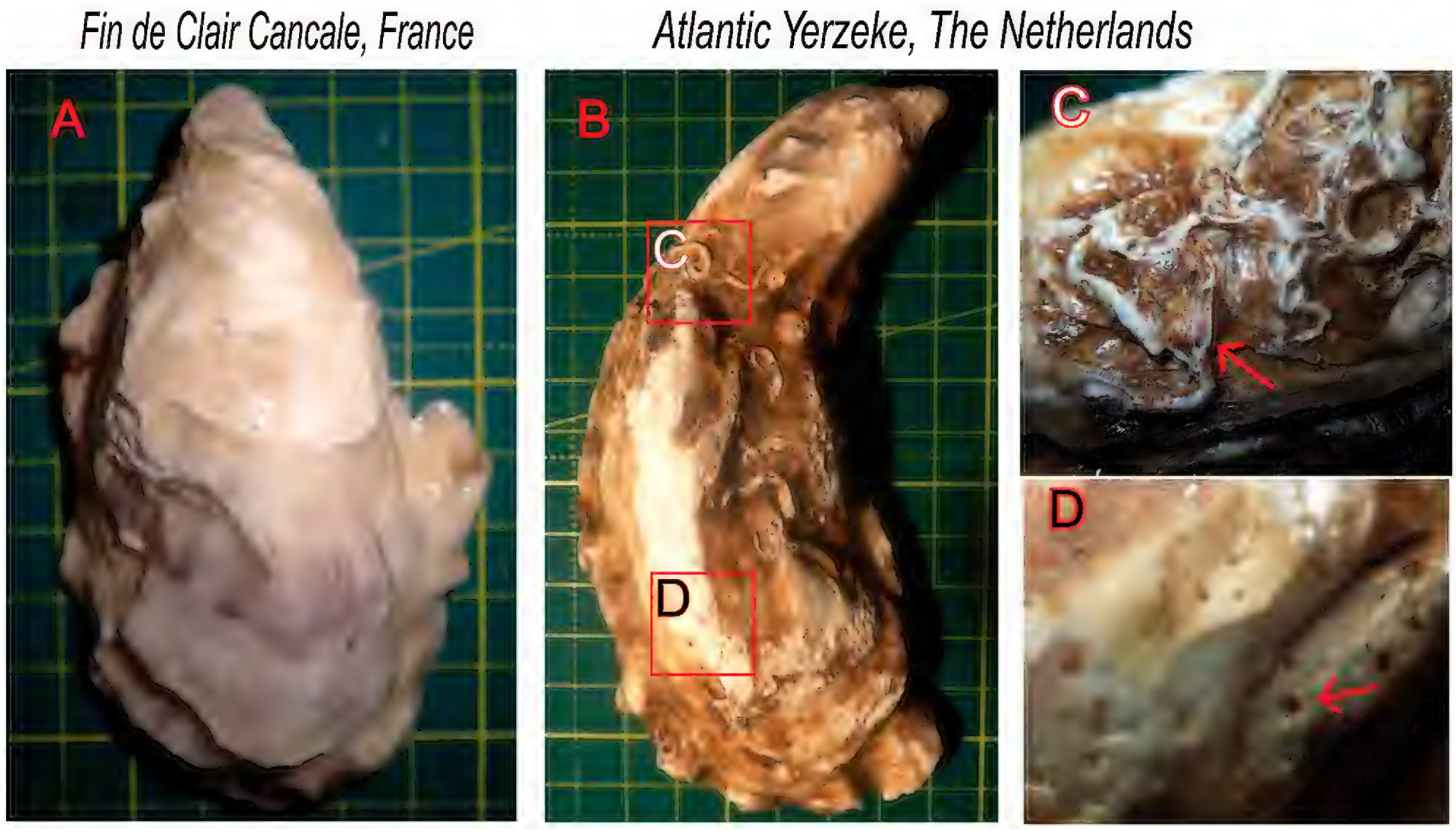

Figure 6. Visual inspections of fouling organisms on Pacific Oysters from various commercial brands and growing regions. **A.** Clean shell with scarper marks from Fin de Clair Cancale France, and **B.** Shell from Atlantic Yerzeke, the Netherlands with **C.** Polychaete tubes (shown by arrow) and **D.** Drilling sponges (shown by arrow).

molluscs, and macroalgae (Adams et al. 2011). The shell is also home to boring polychaetes and sponges which, in addition to their aesthetic impact on the shell, form blisters and erosions that reduce its strength during transport (Mizuta and Wikfors 2019). These can only be removed during the aquaculture process (e.g. by 'dipping' methods and the culture regime itself) or by manual culling of non-merchantable individuals (Adams et al. 2011; Mizuta and Wikfors 2019).

The Ukrainian oyster market is still underdeveloped and has not led to the emergence of a discerning consumer. Inspection of live oysters available for sale, in both the studied tasting point and large supermarkets, showed that while prices for different batches differ considerably according to international quality standards, they are practically the same for a retail buyer. The same shop was found to sell oysters almost completely free of epibionts (with small barnacles inside the shell hollows inaccessible for brushing) with a regular drop-shape and standardised sizes at the same price as multi-sized long and skinny oysters, known as *bunny rabbits* (Fig. 6), which are densely covered with polychaete houses and drilled with numerous sponges. The second group are clearly intended for the frozen meat trade or the preparation of soups, which would be excluded from the live food trade for restaurants or parties in a more developed market.

Such poor oyster consumption traditions increase the risk of transferring live oysters with shells that have not been cleared of epibionts. Hence, another way of reducing the risk of the spread of alien species could be to raise consumer awareness of live food standards. Key aspects on the implementation of public awareness include creating informative posters and other educational materials. As well, local authorities can inform tourists and recreational visitors about the risks posed by invasive species and the importance of proper disposal of oyster shells (Fitzsimons et al. 2020). This can help reduce the unintentional transfer of live hitchhikers on dead shells.

Within specific invasion sites, the risks of invasion can be significantly reduced by periodic manual removal of discarded shells from the bottom of waterways by divers. In the case of the Tylihul estuary, where there is a shortage of solid substrates, it has been observed that introduced organisms take time to spread throughout the water body, and they concentrate directly on discarded shells.

Furthermore, in cases where oysters or their shells are used for construction purposes, such as the creation of artificial reefs, it is crucial to implement decontamination protocols such as treating the oysters or shells to remove any attached organisms or larvae (Cohen and Zabin 2009; Ruesink et al. 2005), developing quarantine and handling procedures, and researching the survival rates of microalgae and other biofilms.

Conclusions

The presence of these invertebrates on oyster shells raises concerns regarding their potential ecological impact on the Tylihul Estuary. The identified species are known to compete with native organisms for resources, potentially disrupting local marine ecosystems. Our findings highlight the need for continuous monitoring and management strategies to mitigate the impact of invasive species in this sensitive environment.

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Additional information

Conflict of interest

The authors have declared that no competing interests exist.

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Use of AI

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Author contributions

Halyna Gabrielczak: conceptualization, data curation, formal analysis, funding acquisition, investigation, methodology, visualization, writing – original draft, writing – review and editing. Mikhail O. Son: conceptualization, funding acquisition, supervision, writing – original draft, writing – review and editing. Yuriy Kvach: funding acquisition, investigation, validation, writing – review and editing.

Author ORCIDs

Halyna Gabrielczak https://orcid.org/0000-0002-7888-477X
Yuriy Kvach https://orcid.org/0000-0002-6122-4150
Mikhail O. Son https://orcid.org/0000-0001-9794-4734

Data availability

All data that support the findings of this study are available in the main text and supplementary materials, as well as in the BOLD System repository, http://www.boldsystems.org. Relevant voucher information is accessible through the public dataset DS-OYSTER (DOI: http://dx.doi.org/10.5883/DS-OYSTER).

References

Adams CM, Shumway SE, Whitlatch RB, Getchis T (2011) Biofouling in marine molluscan shellfish aquaculture: A survey assessing the business and economic implications of mitigation. Journal of the World Aquaculture Society 42(2): 242–252. https://doi.org/10.1111/j.1749-7345.2011.00460.x

Ahmed OO, Solomon OO (2016) Ecological consequences of oyster culture: A review. Journal of Fisheries & Livestock Production 4: 1–6. https://doi.org/10.4172/2332-2608.1000198

Alunno-Bruscia M, Bourles Y, Maurer D, Robert S, Mazurie J, Gangnery A, Goulletquer P, Stephane P (2011) A single bio-energetics growth and reproduction model for the oyster *Crassostrea gigas* in six Atlantic ecosystems. Journal of Sea Research 66(4): 3408. https://doi.org/10.1016/j.seares.2011.07.008

Anglès d'Auriac MB, Rinde E, Norling P, Lapegue S, Staalstrøm A, Hjermann DØ, Thaulow J (2017) Rapid expansion of the invasive oyster *Crassostrea gigas* at its northern distribution limit in Europe: Naturally dispersed or introduced? PLOS ONE 12(5): e0177481. https://doi.org/10.1371/journal.pone.0177481

Avdelas L, Avdic-Mravlje E, Borges Marques AC, Cano S, Capelle JJ, Carvalho N, Cozzolino M, Dennis J, Ellis T, Fernández Polanco JM, Guillen J, Lasner T, Le Bihan V, Llorente I, Mol A, Nicheva S, Nielsen R, van Oostenbrugge H, Villasante S, Visnic S, Zhelev K, Asche F (2021) The decline of mussel aquaculture in the European Union: Causes, economic impacts and opportunities. Reviews in Aquaculture 13(1): 91–118. https://doi.org/10.1111/raq.12465

Aydin M, Gül M (2021) Presence of the Pacific Oyster (*Crassostrea gigas* Thunberg, 1793) in the Black Sea. Journal of Anatolian Environmental and Animal Sciences 6(1): 14–17. https://doi.org/10.35229/jaes.800160

Aydin M, Biltekin D, Breugelmans K, Backeljau T (2021) First record, DNA identification and morphometric characterization of Pacific Oyster, *Crassostrea gigas* Thunberg, 1793 in the southern Black Sea. BioInvasions Records 10(4): 838–852. https://doi.org/10.3391/bir.2021.10.4.08

Băncilă RI, Skolka M, Ivanova P, Surugiu V, Stefanova K, Todorova V, Zenetos A (2022) Alien species of the Romanian and Bulgarian Black Sea coast: State of knowledge, uncertainties, and needs for future research. Aquatic Invasions 17(3): 353–373. https://doi.org/10.3391/ai.2022.17.3.02

Bilecenoğlu M, Yokeş MB, Aydin M (2023) First record of *Sebastes schlegelii* Hilgendorf, 1880 along the Turkish Black Sea coast – new addition to the alien species inventory. Turkish Journal of Maritime and Marine Sciences 9: 119–128. https://doi.org/10.52998/trjmms.1358814

Birney LB, Evans BR, Solanki V, Mojica ER, Scharff C, Kong J (2021) The Billion Oyster Project and curriculum and community enterprise for restoration science curriculum impact on underrepresented student motivation to pursue STEM Careers. Journal of Curriculum and Teaching 10(4): 47–54. https://doi.org/10.5430/jct.v12n4p125

Brumbaugh RD, Coen LD (2009) Contemporary approaches for small-scale oyster reef restoration to address substrate versus recruitment limitation: A review and comments relevant for the

Olympia Oyster, *Ostrea lurida* Carpenter 1864. Journal of Shellfish Research 28(1): 147–161. https://doi.org/10.2983/035.028.0105

Bushek D, Richardson D, Bobo MY, Coen LD (2004) Short-term shell pile quarantine reduces the abundance of *Perkinsus marinus* remaining in tissues attached to oyster shell. Journal of Shellfish Research 23: 369–373.

Carlton JT, Newman WA, Pitombo FB (2011) Barnacle invasions: introduced, cryptogenic, and range expanding Cirripedia of North and South America. In the wrong place-alien marine crustaceans: distribution, biology and impacts: 159–213. https://doi.org/10.1007/978-94-007-0591-3_5

Carranza A, Zu Ermgassen PS (2020) A global overview of restorative shellfish mariculture. Frontiers in Marine Science 7: 722. https://doi.org/10.3389/fmars.2020.00722

Casquet J, Thebaud C, Gillespie RG (2012) Chelex without boiling, a rapid and easy technique to obtain stable amplifiable DNA from small amounts of ethanol-stored spiders. Molecular Ecology Resources 12(1): 136–141. https://doi.org/10.1111/j.1755-0998.2011.03073.x

Chapman JW, Miller TW, Coan EV (2003) Live seafood species as recipes for invasion. Conservation Biology : The Journal of the Society for Conservation Biology 17(5): 1386–1395. https://doi.org/10.1046/j.1523-1739.2003.01016.x

Chetveryk O, Kravchuk N (2020) Doslidzhennia kon'yuktury rynku ustryts: Stan ta perspektyvy rozvytku na zasadakh marketynhu. Bioeconomics and Agrarian Business 11(1): 1–18. [The research or the oyster's market condition: current state and future perspective development on the basis of marketing] [In Ukrainian with English summary]

Chowdhury MS, Walles B, Sharifuzzaman SM, Hossain S, Ysebaert T, Smaal AC (2019) Oyster breakwater reefs promote adjacent mudflat stability and salt marsh growth in a monsoon dominated subtropical coast. Scientific Reports 9(1): 8549–8549. https://doi.org/10.1038/s41598-019-44925-6

Cohen AN, Zabin CJ (2009) Oyster shells as vectors for exotic organisms. Journal of Shellfish Research 28(1): 163. https://doi.org/10.2983/035.028.0106

Convention on Biological Diversity (1995) Convention on Biological Diversity. https://www.cbd.int/convention/

Convention on International Trade in Endangered Species of Wild Fauna and Flora (1999) CITES: Convention on International Trade in Endangered Species of Wild Fauna and Flora. https://www.cites.org/

Council of Europe (1996) Convention on the Conservation of European Wildlife and Natural Habitats (Bern Convention). https://www.coe.int/en/web/bern-convention/home

Coutts A, O'Brien A, Weeks AR, Swearer SE, van Rooyen A, Branigan S, Morris RL (2022) An environmental DNA approach to informing restoration of the functionally extinct oyster, *Ostrea angasi*. Aquatic Conservation 32(11): 1732–1744. https://doi.org/10.1002/aqc.3886

Crickenberger S, Wethey DS (2018) Reproductive physiology, temperature and biogeography: The role of fertilization in determining the distribution of the barnacle *Semibalanus balanoides*. Journal of the Marine Biological Association of the United Kingdom 98(6): 1411–1424. https://doi.org/10.1017/S0025315417000364

Degremont L, Guyader T, Tourbiez D, Pepin JF (2013) Is horizontal transmission of the Ostreid herpesvirus OsHV-1 in *Crassostrea gigas* affected by unselected or selected survival status in adults to juveniles? Aquaculture (Amsterdam, Netherlands) 408: 51–57. https://doi.org/10.1016/j.aquaculture.2013.05.025

Devos A, Dallas LJ, Voiseux C, Lecomte-Pradines C, Jha AN, Fievet B (2015) Assessment of growth, genotoxic responses and expression of stress-related genes in the Pacific Oyster *Crassostrea gigas* following chronic exposure to ionizing radiation. Marine Pollution Bulletin 95(2): 688–698. https://doi.org/10.1016/j.marpolbul.2015.03.039

Di Blasio L, Chiesa S, Arcangeli G, Donadelli V, Marino G (2023) Alien species associated with new introductions and translocations of commercial bivalves in Italian marine waters. Sustainability 15(4): 3536. https://doi.org/10.3390/su15043536

Directive (2000) Directive 2000 /60/EC of the European Parliament and of the Council of 23 October 2000. http://data.europa.eu/eli/dir/2000/60/2014-11-20

Dugal L, Thomas L, Berry TE, Simpson T, Miller K (2024) Environmental DNA metabarcoding for the detection of the Silverlip Pearl Oyster (*Pinctada maxima*) offshore of Eighty Mile Beach in northwest Australia. Estuarine, Coastal and Shelf Science 301: 108722. https://doi.org/10.1016/j.ecss.2024.108722

Dundon WG, Arzul I, Omnes E, Robert M, Magnabosco C, Zambon M, Gennari L, Toffan A, Terregino C, Capua I, Giuseppe A (2011) Detection of Type 1 Ostreid Herpes variant (OsHV-1 mu var) with no associated mortality in French-origin Pacific Cupped Oyster *Crassostrea gigas* farmed in Italy. Aquaculture (Amsterdam, Netherlands) 314(1–4): 49–52. https://doi.org/10.1016/j.aquaculture.2011.02.005

Fitzsimons J, Branigan S, Gillies CL, Brumbaugh RD, Cheng J, DeAngelis B, Geselbracht L, Hancock B, Jeffs A, McDonald T, McLeod I, Pogoda B, Theuerkauf SJ, Thomas M, Westby S, Ermgassen PSE (2020) Restoring shellfish reefs: Global guidelines for practitioners and scientists. Conservation Science and Practice Society for Conservation Biology 2(6): e198. https://doi.org/10.1111/csp2.198

Folmer O, Black M, Hoeh W, Lutz R, Vrijenhoek R (1994) DNA primers for amplification of mitochondrial cytochrome c oxidase subunit I from diverse metazoan invertebrates. Molecular Marine Biology and Biotechnology 3: 294–299.

Gilbey J, Carvalho G, Castilho R, Coscia I, Coulson MW, Dahle G, Derycke S, Francisco S, Helyar S, Johansen T, Junge C, Layton K, Mortinsohn J, Matejusova I, Robalo J, Rodrigue-Ezpeleta N, Silva G, Strammer I, Vasemagi A, Volckaert FA (2021) Life in a drop: Sampling environmental DNA for marine fishery management and ecosystem monitoring. Marine Policy 124: 104331. https://doi.org/10.1016/j.marpol.2020.104331

Glenner H, Lützen J, Pacheco-Riaño LC, Noever C (2021) Expansion of the barnacle *Austrominius modestus* (Darwin, 1854) (Cirripedia, Thoracica, Balanidae) into Scandinavian waters based on collection data and niche distribution modeling. Aquatic Invasions 16(4): 675–689. https://doi.org/10.3391/ai.2021.16.4.06

Gogaladze A, Son MO, Lattuada M, Anistratenko VV, Syomin VL, Pavel AB, Popa OP, Popa LO, ter Poorten JJ, Biesmeijer JC, Raes N, Wilke T, Sands AF, Trichkova T, Hubenov ZK, Vinarski MV, Anistratenko OY, Alexenko TL, Wesselingh FP (2021) Decline of unique Pontocaspian biodiversity in the Black Sea Basin: A review. Ecology and Evolution 11(19): 12923–12947. https://doi.org/10.1002/ece3.8022

Gomoiu MT, Alexandrov B, Shadrin N, Zaitsev Y (2002) The Black Sea — A recipient, donor and transit area for alien species. In: Leppäkoski E, Gollasch S, Olenin S (Eds) Invasive Aquatic Species of Europe Distribution, Impacts and Management. Springer, Dordrecht. https://doi.org/10.1007/978-94-015-9956-6_35

Gozlan RE, Bommarito C, Caballero-Huertas M, Givens J, Mortillaro JM, Pepey E, Purco Ralaiarison R, Senff P, Combe M (2024) A one-health approach to non-native species, aquaculture, and food security. Water Biology and Security 3(2): 100250. https://doi.org/10.1016/j.watbs.2024.100250

Green DS, Crowe TP (2014) Context- and density-dependent effects of introduced oysters on biodiversity. Biological Invasions 16: 1145–1163. https://doi.org/10.1007/s10530-013-0569-x

Grintsov VA (2018) On finding of *Monocorophium insidiosum* Crawford, 1937 (Amphipoda, Corophiidae) in the coastal waters of Crimea (Black Sea), a new species for this region. Morskoj Biologičeskij Žurnal 3(2): 33–39. https://doi.org/10.21072/mbj.2018.03.2.02

Harrower CA, Scalera R, Pagad S, Schönrogge K, Roy HE (2017) Guidance for interpretation of CBD categories on introduction pathways. Technical note prepared by IUCN for the European Commission. https://www.cbd.int/doc/c/9d85/3bc5/d640f059d03acd-717602cd76/sbstta-22-inf-09-en.pdf

Hebert PDN, Stoeckle MY, Zemlak T, Francis CM (2004) Identification of birds through DNA barcodes. Public Library of Science 2(10): e312. https://doi.org/10.1371/journal.pbio.0020312

Hégaret H, Shumway SE, Wikfors GH, Pate S, Burkholder JM (2008) Potential transport of harmful algae via relocation of bivalve molluscs. Marine Ecology Progress Series 361: 169–179. https://doi.org/10.3354/meps07375

Herrera M, Wethey DS, Vázquez E, Macho G (2019) Climate change implications for reproductive success: Temperature effect on penis development in the barnacle *Semibalanus balanoides*. Marine Ecology Progress Series 610: 109–123. https://doi.org/10.3354/meps12832

Hou ZG, Fu JH, Li SQ (2007) A molecular phylogeny of the genus *Gammarus* (Crustacea: Amphipoda) based on mitochondrial and nuclear gene sequences. Molecular Phylogenetics and Evolution 45: 596–611. https://doi.org/10.1016/j.ympev.2007.06.006

Hulme PE (2021) Unwelcome exchange: International trade as a direct and indirect driver of biological invasions worldwide. One Earth 4(5): 666–679. https://doi.org/10.1016/j.oneear.2021.04.015

International Maritime Organization (2004) International Convention for the Control and Management of Ship Ballast Water and Sediments. https://www.imo.org/en/OurWork/Environment/Pages/BallastWaterManagement.aspx

Inui R, Onikura N, Kawagishi M, Nakatani M, Tomiyama Y, Oikawa S (2010) Selection of spawning habitat by several gobiid fishes in the subtidal zone of a small temperate estuary. Fisheries Science 76: 83–91. https://doi.org/10.1007/s12562-009-0192-z

Jones SJ, Southward AJ, Wethey DS (2012) Climate change and historical biogeography of the barnacle *Semibalanus balanoides*. Global Ecology and Biogeography 21(7): 716–724. https://doi.org/10.1111/j.1466-8238.2011.00721.x

Katsanevakis S, Moustakas A (2018) Uncertainty in marine invasion science. Frontiers in Marine Science 5: 38. https://doi.org/10.3389/fmars.2018.00038

Katsanevakis S, Zenetos A, Belchior C, Cardoso AC (2013) Invading European seas: Assessing pathways of introduction of marine aliens. Ocean and Coastal Management 76: 64–74. https://doi.org/10.1016/j.ocecoaman.2013.02.024

Katsanevakis S, Olenin S, Puntila-Dodd R, Rilov G, Stæhr PA, Teixeira H, Tsirintanis K, Birchenough S, Jakobsen H, Khudsen S, Lanzen A, Mazaris A, Piraino S, Tidbury HJ (2023) Marine invasive alien species in Europe: 9 years after the IAS Regulation. Frontiers in Marine Science 10: 1271755. https://doi.org/10.3389/fmars.2023.1271755

Khutornoy S, Kvach Y (2019) First record of the Montague's Blenny (*Coryphoblennius galerita* (L., 1758) (Actinopterygii: Blenniidae) in the mesohaline waters of the North-Western Black Sea, Ukraine. BioInvasions Records 8(4): 917–923. https://doi.org/10.3391/bir.2019.8.4.20

Kim J, Jung D, Lee WS, Park JK (2015) Development of a DNA microarray-based identification system for commercially important Korean oyster species. Journal of Shellfish Research 34(3): 841–847. https://doi.org/10.2983/035.034.0313

Kimbro DL, Stallings CD, White JW (2020) Diminishing returns in habitat restoration by adding biogenic materials: A test using estuarine oysters and recycled oyster shell. Restoration Ecology 28: 1633–1642. https://doi.org/10.1111/rec.13227

Kingsley-Smith PR, Joyce RE, Arnott SA, Roumillat WA, McDonough CJ, Reichert MJ (2012) Habitat use of intertidal Eastern Oyster (*Crassostrea virginica*) reefs by nekton in South Carolina estuaries. Journal of Shellfish Research 31: 1009–1021. https://doi.org/10.2983/035.031.0413

Kochmann J, Crowe TP (2014) Effects of native macroalgae and predators on survival, condition and growth of non-indigenous Pacific Oysters (*Crassostrea gigas*). Journal of Experimental Marine Biology and Ecology 451: 1229. https://doi.org/10.1016/j.jembe.2013.11.007

Kourantidou M, Haubrock PJ, Cuthbert RN, Bodey TW, Lenzner B, Gozlan RE, Nunez MA, Salles JM, Diagne C, Courchamp F (2022) Invasive alien species as simultaneous benefits and burdens: Trends, stakeholder perceptions and management. Biological Invasions 24(7): 1905–1926. https://doi.org/10.1007/s10530-021-02727-w

Krapal AM, Ioniță M, Caplan M, Buhaciuc-Ioniță E (2019) Wild Pacific Oyster *Magallana gigas* (Thunberg, 1793) populations in Romanian Black Sea waters – friend or foe? Travaux du Muséum National d'Histoire Naturelle. Grigore Antipa 62(2): 175–183. https://doi.org/10.3897/travaux.62.e49074

Kurtul I, Haubrock PJ (2024) The need of centralized coordination to counter biological invasions in the European Union. Environmental Sciences Europe 36(1): 129. https://doi.org/10.1186/s12302-024-00955-0

Kvach Y (2004) The helminth fauna of gobiid fishes (Gobiidae) from the Tyligul Estuary of the Black Sea. Visnyk of Lviv University (Biology series) 37: 144–148.

Kvach Y, Khutornoi S (2025) The Korean Rockfish, *Sebastes schlegelii* Hilgendorf, 1880 (Actinopterygii: Scorpaeniformes: Sebastidae) – a new component in the north-western Black Sea coastal fish fauna. BioInvasions Records 14(1):251-259. https://doi.org/10.3391/bir.2025.14.1.19

Kvach Y, Gabrielczak H, Lepekha A, Son MO, Khutornoi S (2025a) The Chesapeake Blue Crab, *Callinectes sapidus* Rathbun, 1896: New finding, origin, and further spread in the Ukrainian part of the Black Sea. Aquatic Invasions 20(2): 199–214. https://doi.org/10.3391/ai.2025.20.2.154614

Kvach Y, Stepien CA, Minicheva GG, Tkachenko P (2025b) Biodiversity effects of the Russia–Ukraine war and the Kakhovka Dam destruction: Ecological consequences and predictions for marine, estuarine, and freshwater communities in the northern Black Sea. Ecological Processes 14(1): 1–25. https://doi.org/10.1186/s13717-025-00577-1

Liu J, Li Q, Kong L, Yu H, Zheng X (2011) Identifying the true oysters (Bivalvia: Ostreidae) with mitochondrial phylogeny and distance-based DNA barcoding. Molecular Ecology Resources 11(5): 820–830. https://doi.org/10.1111/j.1755-0998.2011.03025.x

Makarov YuN (2004) Fauna of Ukraine. Decapoda. Kyiv: Naukova Dumka. Vol. 26, 429 pp.

Markus S, Matejusova I, Douglas A, Sanderson W (2021) Development of eDNA tools for the detection of marine invasive non-native species to support European Flat Oyster (*Ostrea edulis*) restoration projects. ARPHA Conference Abstracts 4: e65383. https://doi.org/10.3897/aca.4.e65383

Massa F, Aydin I, Fezzardi D, Akbulut B, Atanasoff A, Beken AT, Bekh V, Buhlak Y, Burlachenko I, Can E, Carboni S, Caruso F, Dağtekin M, Demianenko K, Deniz H, Fidan D, Fourdain L, Frederiksen M, Guchmanidze A, Hamza H, Harvey J, Nenciu M, Nikolov G, Niţă V, Özdemir MD, Petrova-Pavlova E, Popescu G, Rad F, Can ŞS, Theodorou JA, Thomas B, Tonachella N, Tribilustova E, Yakhontova I, Yesilsu AF, Yücel-Gier G (2021) Black Sea aquaculture: Legacy, challenges and future opportunities. Aquaculture Studies 21(4): 181–220. https://doi.org/10.4194/2618-6381-v21_4_05

Mitov P, Uzunova S, Kenderov L, Dimov S, Yanachkov P (2020) Pacific Oyster invasion along Bulgarian Black Sea coast. Scientific Conference "Kliment's Days", 5th November 2020, Abstracts. Sofia University St. Kliment Ohridski, Faculty of Biology, 55.

Mizuta DD, Wikfors GH (2019) Seeking the perfect oyster shell: A brief review of current knowledge. Reviews in Aquaculture 11(3): 586–602. https://doi.org/10.1111/raq.12247

Molnar JL, Gamboa RL, Revenga C, Spalding MD (2008) Assessing the global threat of invasive species to marine biodiversity. Frontiers in Ecology and the Environment 6(9): 485–492. https://doi.org/10.1890/070064

Montagnani C, Gentili R, Brundu G, Caronni S, Citterio S (2022) Accidental introduction and spread of top invasive alien plants in the European Union through human-mediated agricultural pathways: What should we expect? Agronomy (Basel) 12(2): 423. https://doi.org/10.3390/agronomy12020423

Mortensen S, Strand Å, Bodvin T, Alfjorden A, Skår CK, Jelmert A, Aspán A, Sælemyr L, Naustvoll LJ, Albretsen J (2016) Summer mortalities and detection of ostreid herpes virus microvariant in Pacific Oyster *Crassostrea gigas* in Sweden and Norway. Diseases of Aquatic Organisms 117(3): 171–176. https://doi.org/10.3354/dao02944

Movchan YV (2011) Fishes of Ukraine. Kyiv, Zoloti Vorota. [in Ukrainian]

O'Riordan RM, Culloty SC, Mcallen R, Gallagher MC (2020) The biology of *Austrominius modestus* (Darwin) in its native and invasive range. Oceanography and Marine Biology, CRC Press, 1–78. https://library.oapen.org/handle/20.500.12657/47403. https://doi.org/10.1201/9780429351495-1

Olenin S, Minchin D, Daunys D (2007) Assessment of biopollution in aquatic ecosystems. Marine Pollution Bulletin 55(7–9): 379–394. https://doi.org/10.1016/j.marpolbul.2007.01.010

Oliver GA, McGrath D, Healy B (2007) The amphipod *Corophium insidiosum* Crawford in Ireland. The Irish Naturalists' Journal: 324–326. https://www.jstor.org/stable/25536780

Padilla DK, McCann MJ, Shumway SE (2011) Marine invaders and bivalve aquaculture: sources, impacts, and consequences. In: Shellfish aquaculture and the environment, 395–424. https://doi.org/10.1002/9780470960967.ch14

Panov VE, Alexandrov B, Arbačiauskas K, Binimelis R, Copp GH, Grabowski M, Lucy F, Leuven RSEW, Nehring S, Paunovic M, Semenchenko V, Son MO (2009) Assessing the risks of aquatic species invasions via European inland waterways: From concepts to environmental indicators. Integrated Environmental Assessment and Management 5(1): 110–126. https://doi.org/10.1897/IEAM_2008-034.1

Pejovic I, Ardura A, Miralles L, Arias A, Borrell YJ, Garcia-Vazquez E (2016) DNA barcoding for assessment of exotic molluscs associated with maritime ports in northern Iberia. Marine Biology Research 12(2): 168–176. https://doi.org/10.1080/17451000.2015.1112016

Pergl J, Brundu G, Harrower CA, Cardoso AC, Genovesi P, Katsanevakis S, Lozano V, Perglova I, Rabitsch W, Richards G, Roques A, Rorke SL, Scalera R, Schonrogge K, Stewart A, Tricarico E, Tsiamis K, Vannini A, Vil M, Zenetos A, Roy HE (2020) Applying the Convention on Biological Diversity Pathway Classification to alien species in Europe. NeoBiota 62: 333–363. https://doi.org/10.3897/neobiota.62.53796

Petrolia DR, Mohrman T (2024) Oyster shell recycling: Challenges and opportunities for reef restoration. Journal of Shellfish Research 43(3): 361–370. https://doi.org/10.2983/035.043.0307

Png-Gonzalez L, Ramalhosa P, Gestoso I, Álvarez S, Nogueira N (2021) Non-indigenous species on artificial coastal environments: Experimental comparison between aquaculture farms and recreational marinas. Journal of Marine Science and Engineering 9(10): 1121. https://doi.org/10.3390/jmse9101121

Prakash S, Kumar A (2025) Life in the dead shell: Utilization of dead *Pinna* shells by the Blenny Fish *Petroscirtes variabilis* Cantor, 1849 (Blennidae). Science and Nature 112: 9. https://doi.org/10.1007/s00114-025-01960-w

Quayle DB (1964) Distribution of introduced marine mollusca in British Columbia waters. Journal of the Fisheries Research Board of Canada 21(5): 1155–1181. https://doi.org/10.1139/f64-102

Ratnasingham S, Hebert PDN (2013) A DNA-based registry for all animal species: The Barcode Index Number (BIN) system. PLOS ONE 8(7): e66213. https://doi.org/10.1371/journal.pone.0066213

Ren J, Hou Z, Wang H, Sun MA, Liu X, Liu B, Guo X (2016) Intraspecific variation in mitogenomes of five *Crassostrea* species provides insight into oyster diversification and speciation. Marine Biotechnology 18: 242–254. https://doi.org/10.1007/s10126-016-9686-8

Roque A, Carrasco N, Andree KB, Lacuesta B, Elandaloussi L, Gairin I, Rodgers CJ, Furones MD (2012) First report of OsHV-1 microvar in Pacific Oyster (*Crassostrea gigas*) cultured in Spain. Aquaculture (Amsterdam, Netherlands) 324: 303–306. https://doi.org/10.1016/j.aquaculture.2011.10.018

Ruesink JL, Lenihan HS, Trimble AC, Heiman KW, Micheli F, Byers JE, Kay MC (2005) Introduction of non-native oysters: Ecosystem effects and restoration implications. Annual Review of Ecology, Evolution, and Systematics 36: 643–689. https://doi.org/10.1146/annurev.ecolsys.36.102003.152638

Schmitt P, Santini A, Vergnes A, Degremont L, de Lorgeril J (2013) Sequence polymorphism and expression variability of *Crassostrea gigas* immune-related genes discriminate two oyster lines contrasted in terms of resistance to summer mortalities. PLOS ONE 8(9): e75900. https://doi.org/10.1371/journal.pone.0075900

Shadrin NV, Anufriieva EV (2013) Climate change impact on the marine lakes and their crustaceans: The case of marine hypersaline Lake Bakalskoye (Ukraine). Turkish Journal of Fisheries and Aquatic Sciences 13(4): 603–611. https://doi.org/10.4194/1303-2712-v13_4_05

Snigirov S, Bushuev S, Chernikov G, Kovtun O, Zamorov V, Kurakin A (2017) Ichthyofauna of the Tiligulskiy Lyman (Estuary) in the beginning of XXI century. Ukrainian Journal of Ecology 7(4): 35–45. [in Ukrainian] https://doi.org/10.15421/2017_84

Snigirov SM, Zamorov VV, Karavanskyi YV, Pitsyk VZ, Kurakin OP, Abakumov OM, Liumkis PV, Snigirov PM, Morozov YV, Kvach Y, Kutsokon YK (2020) Taxonomic and eco-faunistic features of the nowadays fish fauna of the Gulf of Odesa, the Dniester mouth forefront near-shores and coastal waters of the Snake (Zmiinyi) Island. Odesa National University Herald (Ser. Biology) 25(2): 113–139. [in Ukrainian] https://doi.org/10.18524/2077-1746.2020.2(47).218060

Son MO, Novitsky RA, Dyadichko VG (2013) Recent state and mechanisms of invasions of exotic decapods in Ukrainian rivers. Vestnik Zoologii 47(1): 59–64.

Son MO, Bondarenko O, Kvach Y (2023) New data on aquatic alien invertebrates in the Ukrainian Danube Delta with special emphasis on the first records of the Trumpet Ram's-horn, *Menetus dilatatus* (Gould, 1841). BioInvasions Records 12(3): 787–795. https://doi.org/10.2478/vzoo-2013-0004

Tan K, Ya P, Tan K, Cheong KL, Fazhan H (2023) Ecological impact of invasive species and pathogens introduced through bivalve aquaculture. Estuarine, Coastal and Shelf Science 294: 108541. https://doi.org/10.1016/j.ecss.2023.108541

Theuerkauf SJ, Barrett LT, Alleway HK, Costa-Pierce BA, Gelais AS, Jones RC (2022) Habitat value of bivalve shellfish and seaweed aquaculture for fish and invertebrates: Pathways, synthesis and next steps. Reviews in Aquaculture 14(1): 54–72. https://doi.org/10.1111/raq.12584

Tiralongo F, Tibullo D, Brundo MV, Paladini De Mendoza F, Melchiorri C, Marcelli M (2016) Habitat preference of Combtooth Blennies (Actinopterygii: Perciformes: Blenniidae) in very shallow waters of the Ionian Sea, south-eastern Sicily, Italy. Acta Ichthyologica et Piscatoria 46(2): 65–75. https://doi.org/10.3750/AIP2016.46.2.02

Troost K (2010) Causes and effects of a highly successful marine invasion: Case-study of the introduced Pacific Oyster *Crassostrea gigas* in continental NW European estuaries. Journal of Sea Research 64(3): 145–165. https://doi.org/10.1016/j.seares.2010.02.004

Tsiamis K, Cardoso AC, Gervasini E (2017) The European alien species information network on the convention on biological diversity pathways categorization. NeoBiota 32: 21–29. https://doi.org/10.3897/neobiota.32.9429

TSN (2020) A unique eco-project at the bottom of the Black Sea: an artificial reef has been created on the Kinburn Spit. https://tsn.ua/ukrayina/unikalniy-ekoproekt-na-dni-chornogo-morya-na-kinburnskiy-kosi-stvorili-shtuchniy-rif-1626658.html [Accessed on 2025-03-20] [In Ukrainian]

Tuchkovenko YS, Loboda NS [Eds] (2014) Water Resources and Hydro-Ecological Regime of the Tyligulskyi Liman Lagoon - Odessa. Odessa State Environmental University, 278 pp.

United Nations Environment Programme (1994) Convention on the Protection of the Black Sea against Pollution. https://www.blacksea-commission.org/

Varigin AY (2023) Specific features of the macrozoobenthos condition in the Tylihul Estuary (Northern Black Sea) in 2021. Marine Ecology Journal 1–2: 7–15. [In Ukrainian with English summary] https://doi.org/10.47143/1684-1557/2023.1-2.1

Verlaque M, Boudouresque CF, Mineur F (2007) Oyster transfers as a vector for marine species introductions: a realistic approach based on the macrophytes. CIESM Workshop Monographs, Monaco, February 2007, Vol. 32, 39–48.

Walles B, Mann R, Ysebaert T, Troost K, Herman PM, Smaal AC (2015) Demography of the ecosystem engineer *Crassostrea gigas*, related to vertical reef accretion and reef persistence. Estuarine, Coastal and Shelf Science 154: 224–233. https://doi.org/10.1016/j.ecss.2015.01.006

Wasson K, Zabia CJ, Bedinger L, Diaz MC, Pearse JS (2001) Biological invasions of estuaries without international shipping: The importance of intraregional transport. Biological Conservation 102: 143–153. https://doi.org/10.1016/S0006-3207(01)00098-2

Yağlıoglu D, Doğdu SA, Turan C (2023) First morphological and genetic record and confirmation of Korean Rockfish *Sebastes schlegelii* Hilgendorf, 1880 in the Black Sea coast of Türkiye. ESciences 8: 140–150. https://doi.org/10.28978/nesciences.1363941

Zaharia T, Crivăț M (2017) Creşterea dirijată a stridiei japoneze (*Crassostrea gigas*) la litoralul românesc. In: Zaharia T, Niță VN, Nenciu MI (Eds) Bazele acvaculturii marine în România. CD PRESS, Bucureşti, 28–49.

Zaitsev YP, Alexandrov BG (1998) Black Sea biological diversity. United Nations Publications, New York.

Zaitsev Y, Mamaev V (1997) Marine biological diversity in the Black Sea: a study of change and decline. (Black sea Environmental series, 3). UN, New York, 208 pp.

Zhulidov AV, Kozhara AV, Son MO, Morhun H, van der Velde G, Leuven RSEW, Gurtovaya TY, Zhulidov DA, Kalko EA, Kuklina YA, Kosmenko LS, Santiago-Fandino VJR, Nalepa TF (2021) Additional records of the bivalves *Mytilopsis leucophaeata* (Conrad, 1831) (Dreissenidae) and *Arcuatula senhousia* (Benson, 1842) (Mytilidae) in the Ponto-Caspian region. BioInvasions Records 10(1): 119–135. https://doi.org/10.3391/bir.2021.10.1.14

Zolotarev V (1996) The Black Sea ecosystem changes related to the introduction of new mollusc species. Marine Ecology (Berlin) 17: 227–236. https://doi.org/10.1111/j.1439-0485.1996.tb00504.x

Supplementary material 1

Occurences and phylogenetic data

Authors: Halyna Gabrielczak

Data type: xlsx

Explanation note: Occurences and phylogenetic data on *Magallana gigas* and *Monocorophium insidiosum* from public repositories used to generate Fig. 2.

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